Directional asymmetry of facial and limb traits in horses and ponies

Kirsty Leśniak *

Centre for Performance in Equestrian Sports, Hartpury College, Hartpury, Gloucester GL19 3BE, England, UK

* Corresponding author. Tel.: +44 1452 702488.
E-mail address: kirsty.lesniak@hartpury.ac.uk (K. Leśniak).

Abstract

Current published data referring to directional asymmetry (DA) of horses refer to racing Thoroughbreds. The aim of this study was to identify whether horses and ponies exhibit directionality of trait asymmetries. Eleven functional (limb) and four non-functional (facial) bilateral traits were measured on left and right sides in a cohort of 100 horses and ponies using callipers. The population was investigated as pooled data and as horse (withers height > 148 cm) and pony (withers height ≤ 148 cm) sub-groups. Within the pooled data, functional traits were longer on the right for the third metacarpal (MCIII, 73%) and metatarsal (MTIII, 65%) bones and wider on the left for the forelimb proximal phalanx (54%), MCIII (40%), MTIII (51%) and hind limb proximal phalanx (55%). Dimensions of the intercarpal and tarsocrural joints were larger on the right side. Differences in DA were present between horses and ponies within non-functional traits, but not functional traits. The results suggest that DA within horses and ponies is more likely to be a species trait rather than one exclusive to racing as a result of pressures from directionally orientated training or from selective breeding strategies.

Keywords: Equine; Conformation; Asymmetry; Skeletal; Laterality

Introduction

Symmetry within nature is thought to reflect the ability to defend against environmental or genetic stressors (Moller, 1990, 1993; Hosken, 2001). The ability of an individual's genotype to defend against these stressors is depicted through the symmetry of their phenotype (Tuyttens, 2003). Within bilaterally paired traits, fluctuations from the ideal symmetrical state, with no directional bias, are known as fluctuating asymmetries (FA) or phenodeviants (Van Valen, 1962; Moller 1993; Wilson and Manning, 1996). FA has been used to measure the level of developmental stability within populations and within individuals (Thornhill and Gangestad, 1994). Although the optimum state for an individual is unknown, it is generally assumed that this should be perfect symmetry (Houle, 2000).

Within a population, a mean of zero and a normal distribution around this mean should be observed for differences between left and right sides (Van Valen, 1962). FA in the region of 1-2% of character size is usually exhibited by a population (Gangestad and Thornhill, 1999). A further indicator of imbalanced development is the measure of directional asymmetry (DA), which identifies a skewed distribution of asymmetry to the left or right side. DA has not been linked to developmental stability, but has been suggested to depict an adaptive or functional asymmetry (Tuyttens, 2003).

The athletic phenotype affects performance, with influential features including intermandibular width and length of the third metacarpal bones (Delahunty and Webb, 1991; Mostert and Householder, 2000). Symmetry of bilateral traits influences performance capabilities, especially for Thoroughbred racehorses. Dalin et al. (1985) correlated performance and asymmetries of sacral tuber height in racehorses and demonstrated that greater asymmetry was associated with decreased performance. However, the study by Dalin

et al. (1985) did not consider the origin of asymmetry. The relationship between asymmetry of skeletal dimensions and performance in horses has not been studied.

Traits of lesser functional importance often display greater asymmetry than functional traits (Markow and Clarke, 1997; Moller, 1993). In a sample of 285 children in the Jamaican Symmetry Project, upper body bilateral traits exhibited greater asymmetry than lower body bilateral traits (Trivers et al., 1999). Lower ranking Thoroughbred racehorses exhibit greater asymmetry of non-functional facial traits than the functional limb traits (Manning and Ockenden, 1994).

The effects of limb length discrepancies on gait have been investigated more extensively in humans than horses; the magnitude of the discrepancy has a strong bearing on gait kinematics and kinetics (Bloedel and Hauger, 1995). Limb length discrepancies < 15 mm rarely have clinical implications, whereas discrepancies of greater magnitude lead to dysfunction and pain (Subotnick, 1976). Limb length affects leverage during locomotion; therefore an economical and symmetrical gait is achieved only with symmetrical body traits (Vagenas and Hoshizaki, 1992).

Watson et al. (2003) reported longer right third metacarpal (MCIII) lengths than left, in 76% of racing Thoroughbreds. This was considered to be a consequence of human selection rather than imbalances induced by training stresses, since growth of the MCIII bone ceases by 7 months of age (Thompson, 1995) and therefore should not be affected by subsequent training. Femoral epicondylar dimensions in Thoroughbred racehorses run on a clockwise track are greater for the left than the right limb (Pearce et al., 2005). Runners on an anticlockwise track are presumed to have a mechanical advantage if their outside (right) limb

is longer (Watson et al., 2003). This finding might help explain why horses successful on an anticlockwise track may not be as successful on a clockwise track (Williams and Norris, 2003). As a dynamic structure, bone responds to the forces placed upon it and alternative theories suggest that repeated directionality could also be causal in the development of equine asymmetries (Drevemo et al., 1980; Scutt and Manning, 1996).

Currently the only data that exists regarding directional asymmetry of horses are based on populations of racing Thoroughbreds. The aim of this study was to compare the magnitude and direction of asymmetry within functional and non-functional traits of non-racing horses and ponies.

Materials and methods

The study population consisted of male and female horses and ponies of a variety of breeds at two equestrian centres and two livery yards in Gloucestershire, UK. None of the horses or ponies had an elite competitive record and all were > 5 years of age to eliminate age related changes in symmetry (Trivers et al., 1999). One-hundred horses and ponies were selected via a convenience sampling technique and were investigated both as pooled data and following separation into horses (withers height > 148 cm; $n = 57$) and ponies (withers height ≤ 148 cm; $n = 43$). The data were reviewed as pooled data, as well as separately for horses and ponies.

Direct measurements of 11 functional and four non-functional bilateral traits (Table 1) were determined using Invicta metric callipers (1 mm accuracy), similar to previous studies (Manning and Ockenden, 1994; Manning and Pickup, 1998). The horses and ponies were made to stand squarely on level concrete while being measured; three measurements were

taken at each site by one assessor and a repeated measures one-way analysis of variance (ANOVA) was used to determined intra-observer variability. Two observers repeated the measurements for selected horses following the same protocol and inter-observer repeatability (r) was calculated using the following equation (Lessells et al., 1987):

$$r = s^2_A / (s^2 + s^2_A)$$

where s^2_A is the between-group variance and s^2 is the within-group variance

Absolute (directional) asymmetries (A) were calculated by subtracting the mean of the left trait (L) from the mean of the right trait (R) (A = L-R) (Manning and Pickup, 1998). Positive values indicated a larger left sided trait and negative values indicated a larger right sided trait. Thus, the study determined the directionality of the data rather than the magnitude of the asymmetry in terms of frequencies; outliers were not removed. The directionality of the data was examined using two-way classification χ^2 analysis with significance declared at $P < 0.05$ to test the assumption that, if no directional bias exists, the distribution frequency of left and right for each trait should be equal.

Results

On repeated measures one-way ANOVA, there were significant variances between the three repeated measures for the length of the hind limb proximal phalanx (HPP; $P \leq 0.05$). However, repeatability calculations were 0.99-1.00 for all traits.

There were significant differences between the observed and expected values for the frequency of directionality of asymmetry within the pooled group data ($\chi^2 = 39.8$, degrees of

133 freedom, df = 14, $P \leq 0.05$) and the pony sub-group ($\chi^2 = 31.3$, df = 14, $P \leq 0.05$), but not for
134 the horse sub-group ($\chi^2 = 18.5$, df = 14, $P \geq 0.05$).
135
136 Higher frequencies within bilateral facial traits were recorded for greater length and
137 width on the left (PDA) (Table 2; Fig. 1). Mean trait values tended to be greater for the left
138 traits within those exhibiting PDA and greater on the right for those exhibiting NDA (Table
139 2); however, this was not seen for pinna length in the pony sub-group, where those exhibiting
140 PDA had a greater mean value right sided trait, indicating that, although there were fewer
141 individuals with PDA of this trait, the magnitude of the asymmetries was greater.
142
143 Left forelimb proximal phalanx (FPP) length and width dimensions were frequently
144 larger than observed for the right for the pooled group and the two sub-groups (Table 2).
145 Tendency for a longer right MCIII was greater in all three groups; however the pony sub-
146 group displayed more individuals with greater width on the left whilst the horse sub-group
147 exhibited more individuals with greater width on the right. For all groups the carpal width and
148 depth dimensions were more frequently larger in the right limb. The mean trait values tended
149 to be greater for the left trait within those exhibiting PDA, and greater on the right for those
150 exhibiting NDA; however this was not seen for MCIII length in the pooled data set where
151 those exhibiting PDA had a greater mean value right sided trait or for the carpal depth in the
152 horse data set where those exhibiting NDA had a greater mean value left side, again
153 indicating a lower frequency of incidence but greater individual magnitude of asymmetries.
154
155 Hind limb traits displayed high frequencies of directional asymmetry (Fig. 2). More
156 individuals within all three groups demonstrated greater right HPP length but greater left HPP
157 width. Similarly to the MCIII and to the HPP, a longer third metatarsal (MTIII) bone was

more frequently observed on the right, whilst the greater width of the same trait was more frequently observed in the left limb for all three groups. Tarsal joint width also demonstrated directionality with the right side being larger. As with some of the previous traits, although NDA was observed the mean value for the left side was larger.

Discussion

Asymmetries of non-functional traits may be more common and of greater magnitude than those found within functional traits (Trivers et al., 1999). Low facial trait FA has been correlated with elite performance in humans (Manning and Pickup, 1998) and horses (Manning and Ockenden, 1994; McDonald and Dumbell, 2008). Although pinna asymmetries have no direct functional significance, they potentially reflect factors negatively affecting auditory perception, such as external auditory meatus and middle ear structure malformations. Pinna asymmetries in humans have been linked to auditory canal defects and conductive deafness (Manning et al., 1997). Such developmental defects may negatively affect decoding of audio signals by influencing the passage of sensory information to the cerebral hemispheres and co-ordination of voluntary and involuntary activities. The combination of inadequately functioning cerebral hemispheres and inner ear dysfunction, important for aptitude of balance, may be sufficient enough for the individual to lack optimal balance and co-ordination for high performance potential.

Pinna length exhibited NDA in both the horse sub-group and the pooled group but not the pony sub-group. PDA of pinna length in female human beings has been linked to increased symmetry of offspring (Manning et al., 1997). However, NDA has been reported in a group of elite male athletes, although the possible implications of this finding have not been discussed (Manning and Pickup, 1998). Composed of soft tissue and cartilage, asymmetry of

soft tissues in the human pinna is affected by hormonal fluctuations (Scutt and Manning, 1996) unlike the more cartilaginous pinna of horses. Human findings suggest a link to both sex and performance; these factors were not considered in our study. However, sex differences have been associated with equine laterality previously (McGreevy and Rogers, 2004; Murphy and Arkins, 2004); lateralisation of the horse is linked to cerebral hemispheric lateralisation and therefore a link could exist between motor laterality, pinna symmetry and brain lateralisation.

An almost equal split of PDA and NDA was demonstrated for nostril width within all three groups. Although the anatomical markers used to measure this trait were chosen to reduce the influence of flare, this physiological response to novel stimuli was considered to have an impact on the results for this trait, as was indicated by the standard deviation values in comparison with the means. PDA was observed at a greater frequency for nostril length and width within the pooled and the horse sub-group, but only for nostril width in the pony sub-group. Lateralised nostril use has been identified in species such as the domestic fowl where the young respond to imprinting odours through head shaking after using their right nostril (Vallortigara and Andrew, 1994; Olka and Turkewitz, 2001); a lateralisation link may also exist within the current study. Mixed sex populations of horses have previously demonstrated right nostril preferences during olfactory stimulus tests to novel objects (McGreevy and Rogers, 2004); no sex or age bias for nostril preference was reported, although males were deemed to be more strongly lateralised than the females. Nostril use may be an indicator of sensory lateralisation to novel stimuli (McGreevy and Rogers, 2004), and dominance of the right cerebral hemisphere, involved with processing novel stimuli. The link between nostril asymmetry and the neurological processing of novel stimuli has yet to be confirmed but given similar findings for other sensory organs and motor structures, a link between nostril

asymmetry, nostril laterality and right-side cerebral dominance is proposed for the current results.

A higher frequency of PDA was demonstrated for length and width of the FPP within all three groups. For all three groups, the right MCIII was more frequently greater in length whilst the left MCIII was greater in width. The NDA of MCIII length reflects previous findings, including the results of Watson et al. (2003), where the right MCIII was longer than the left for 76% of Thoroughbred racehorses studied. The longer right limbs were suggested to provide a locomotory advantage over PDA due to the mechanical requirements involved in running in an anti-clockwise direction; as seen on most racecourses. The tendency for the right limb to be longer was present regardless of the direction in which the horses raced. This supports the findings of the current investigation, further intimating that DA is a species trait rather than one developed through selective breeding of racehorses. The difference between the measurement techniques and the individual observers used in the current study and the study by Watson et al. (2003) study potentially mean the magnitude of the data would differ; however, the directionality should not, enabling the directionality of the two sets of data to be compared.

The dimensions of the femoral epicondyle in Thoroughbred racehorses run on a clockwise track are greater on the left than the right (Pearce et al., 2005). Although this potentially indicates bone adaptation due to increased loading of the outside limb during clockwise racing, similar PDA of bone widths were found in the current study and could demonstrate a normal DA within the species rather than the adaptive response to exercise suggested previously (Pearce et al., 2005). Predisposition for injury is greater in the shorter left limb due to potential compensatory gait mechanisms, whereby the horse shortens the

stance phase and lengthens the break over-phase of the longer limb to prevent excess bending of the longer left bone; consequentially landing is heavier on the shorter limb (Davies and Watson, 2005; Perttunen et al., 2004).

McGreevy and Rogers (2004) investigated motor and sensor laterality in Thoroughbreds and identified a preference for advanced left limb placement during grazing; this trend strengthened with age. They suggested that the non-advanced limb bore more weight; however, this could be argued, depending on the individual's stance. The non-advanced limb is often stretched under the body, with weight borne through the dorsal aspect, but the advanced limb often carries the majority of the horse's bodyweight and is therefore under greater compressive forces. As an alternative theory, horses may naturally advance the shorter limb and angle the longer limb under the body to attain the grazing position. This differing hypothesis would support the finding of the longer right limb in the current study. The additional compressive strain on the shorter left limb would result in thickening of the bone over time due to remodelling of this dynamic structure, again reflecting the wider bone dimensions seen within the current study. Lateralisation may be determined in utero (Murphy and Arkins, 2004) and has been suggested, alongside gait habits, to influence bone thickness; however this appears to be in spite of limb asymmetries rather than as a synergistic effect of the asymmetry (Davies and Watson, 2005)

NDA of carpal joint traits was demonstrated by all three groups. Although structurally dissimilar, the human knee joint would have the most similar role within locomotion to the equine carpal joint. A similar NDA of the human knee joint width was identified by Trivers et al. (1999). Auerbach and Ruff (2006) reported NDA of the mediolateral breadth of the femoral epicondyle in the adult human; a principal structure within the human knee. Although

no hypotheses for these findings were given, they may reflect the increase in stability needed to compensate for the longer humeral length observed for the same limb, similar to the longer right MCIII observed in the current study.

HPP width demonstrated a tendency for PDA, as also seen in the FPP; however HPP length demonstrated greater predisposition for NDA. This supports the forelimbs results where the trait is wider on the shorter, left limb as well as previous research findings where a greater propensity for NDA has been reported for length (Watson et al., 2003). However, the measurement of this trait demonstrated significant variance ($P \leq 0.05$) and therefore the results for the length of the HPP could be questioned without further analysis using a more repeatable measurement technique.

DA tendencies of the MTIII reflect those observed for the MCIII and HPP, where the right limb is longer, but the left limb is greater in width. A high percentage of individuals displayed zero asymmetry for MTIII width (pony 26%, horse 19%, pooled group 22%) compared to the other traits. McGreevy and Rogers (2004) suggest that hind limbs demonstrate a more ambidextrous nature than the forelimbs; however Meij and Meij (1980) previously reported a strong left hind limb preference within the majority (83%) of their study group.

The propensity for NDA of the tarsal width did not follow the same PDA trend observed for the widths of the previous limb traits. In humans suffering from limb length discrepancies, compensation mechanisms are observed within the knee and the ankle joints of the longer limb (Walsh et al., 2000). Whether similar compensation mechanisms exist within the tarsal and carpal joint of the horse, resulting in osteophytic changes within the joints of the

longer limb, is an area devoid of research; future investigation could give insight into the effect of limb length discrepancies on the degeneration of the equine tarsal joint.

In other species, reduced heterozygosity has been linked to developmental instability and an increase in bilateral trait asymmetry (Babbitt, 2006; Fessehaye et al., 2007). A reduction in the heterozygosity of the Thoroughbred population exists as a result of modern breeding strategies; thus symmetry of this breed should be reduced, as has been demonstrated in previous equine asymmetry research (Watson et al, 2003; Davies and Watson, 2005; Pearce et al, 2005). These studies have been undertaken mainly in racing Thoroughbreds, where authors have concluded that asymmetry results from adaptive stresses or as a consequence of breeding strategies (Watson et al, 2003; Pearce et al, 2005); as such, they are brought in to question by the current results which are from a population with higher heterozygosity and which should therefore, in theory, show lower asymmetry across the population.

Conclusions

The current findings suggest that the horse is naturally subject to a degree of DA. Further stress related asymmetry may occur in addition to, but not instead of, this naturally occurring asymmetry. It is not possible from this investigation to identify whether this asymmetry is genetically influenced, but these results support the suggestion that lateralisation is determined in utero. The bilateral traits within this study demonstrated persuasive evidence that the right side traits are generally longer, while left side traits are wider. The naturally occurring DA in this study may help to explain why many horses are reported to have an asymmetry of movement, or functional asymmetry. Regardless of the cause or the potential underlying characteristics, the findings from the current study suggest that, for horses and ponies, DA may be the optimum for certain traits, rather than the

presumed optimum of symmetry. A laterality preference, rather than a training influenced directionality could be influential in physical asymmetry.

Conflict of interest statement

The author of this paper does not have a financial or personal relationship with other people or organisations that could inappropriately influence or bias the content of the paper.

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448 **Table 1**

449 Bilateral traits measured including description.

450

Trait	Description
Third metacarpal length (MCIII) and third metatarsal length (MTIII)	Measured laterally from the 'V' formed by the overlap of the annular ligament over the superficial digital flexor tendon at the distal portion of the limb, to the protrusion of the fourth metacarpal/ metatarsal at the proximal region of the distal limb
Third metacarpal width (MCIII) and third metatarsal width (MTIII)	Measured on the horizontal axis half way between the carpometacarpal /tarsometatarsal joint and the metacarpophalangeal /metatarsophalangeal joints
Fore proximal phalanx length (FPP) and hind proximal phalanx length (HPP)	Measured laterally from the protuberance of the lateral cartilage of the distal phalanx to the lateral protrusion made by the proximal condyle of the proximal phalanx
Fore proximal phalanx width (FPP) and hind proximal phalanx width (HPP)	Measured horizontally at the narrowest point of the phalanx
Carpal joint width	Measured horizontally from the medial to the lateral aspects of the intercarpal joint
Carpal joint depth	Measured laterally from the dorsal aspect of the intermediate carpal bone to the palmer aspect of the accessory carpal bone
Tarsal joint width	Measured horizontally from the medial to the lateral aspects of the tarsocrural joint
Pinna length	Measured from the point at the summit of the pinna to the inverted point at the base of the pinna
Pinna width	Measured from the medial to the lateral aspect of the pinna at the midpoint of its length.
Nostril length	Measured from the top of the fold on the medial aspect of the nostril to the lowest point of the nostril
Nostril widths	The width of the nostrils was measured horizontally from the alar fold on the medial aspect to reduce the impact of nasal flaring, to the lateral border of the nostril

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452

Table 2

Distribution of facial trait directional asymmetries as absolute numbers and percentage values; the larger values and therefore the directional asymmetry is highlighted in bold with *P* values to illustrate levels of significance.

	Ponies (%)			Horses (%)			Pooled (%)		
	Left larger	Right larger	No asy-mmetry	Left larger	Right larger	No asy-mmetry	Left larger	Right larger	No asy-mmetry
Pinna length	**53**	33	15	45	**49**	6	**48**	42	10
Pinna width	**65***	28	8	**51**	37	12	**57***	33	10
Nostril length	45	**48**	8	**55**	36	9	**51**	41	8
Nostril width	**51**	39	10	**50**	38	13	**51**	38	11
FPP length	**26**	16	1	**70*****	23	7	**66*****	29	5
FPP width	**22**	14	7	**53**	33	14	**52***	33	15
MCIII length	10	**30*****	3	25	**68*****	7	24	**69*****	7
MCIII width	**15**	12	16	40	**42**	18	**38**	36	26
Carpal width	7	**27*****	9	39	**47**	14	29	**54****	17
Carpal depth	17	**21**	5	46	**49**	6	43	**49**	8
HPP length	18	**23**	2	48	**50**	2	45	**52**	3
HPP width	**23**	14	6	**47**	40	13	**50**	37	13
MTIII length	12	**31****	0	41	**57**	2	35	**64****	1
MTIII width	**20**	10	13	**49**	33	18	**48***	29	23
Tarsal width	8	**30*****	5	42	**46**	13	31	**55****	12

One-way $\chi 2$ analysis using Yates correction (df. 1)

FPP, fore proximal phalanx; HPP, hind proximal phalanx; MCIII, metacarpal III; MTIII, metatarsal III.

*$P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

462 **Figure legends**

463

464 Fig. 1. Asymmetry means including standard deviations for the non-functional (facial) traits
465 of the pooled, horse and pony groupings for both the positive and negative directional
466 asymmetry categories.

467

468 Fig. 2. Asymmetry means including standard deviation for the functional (limb) traits of the
469 pooled, horse and pony groupings for both the positive and negative directional asymmetry
470 categories. FPP, fore proximal phalanx; HPP, hind proximal phalanx; MCIII, metacarpal III;
471 MTIII, metatarsal III.